

Functional Morphology of Feeding Apparatus of the Cookie-Cutter Shark, *Isistius brasiliensis* (Elasmobranchii, Dalatiinae)

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ABSTRACT—External morphology, skeletons, and muscles related to the peculiar feeding mechanism of *Isistius brasiliensis* are described and compared with other squaloid sharks. On the feeding function of this shark, a few characteristic conditions have been emphasized (e.g., fleshy oral margins, scoop-like lower jaw with a sharp tooth row, and developed basihyal and throat muscle). Serious morphological differences are, however, found in the whole of neurocranium, viscerocranium, shoulder girdle, and related musculature. These characteristic conditions are not suitable for the clutching-cutting feeding mechanism of typical squaloids but should effectively work on scooping the flesh of preys, making a strong oral vacuum, and rotating the body itself. These functions explain the cause of a crater-like wound on fish and cetaceans, and *Isistius* must apply them not only on large preys but on small fish and squids.

INTRODUCTION

The cookie-cutter shark, *Isistius brasiliensis* (Quoy et Gaimard), is a pelagic species of worldwide distribution throughout tropical and temperate waters. Among squaloid members, it is rather small reaching a size of 50 cm TL. Recently this shark attracted many oceanological and fishery scientists because of its curious feeding habit revealed by Jones [1]. *Isistius brasiliensis* often feeds by biting chunks out of teleostean swimmers (e.g., dolphinfish, marlin, tuna, albacore, and wahoo), cetaceans, seals, and large pelagic sharks including the megacasmids [1–5]. This small shark gives these preys a crater-like wound, which has been thought to be caused by the bacteria, parasites, or cyclostomes [6]. The purpose of this unusual feeding habit is ambiguous, because *Isistius*'s stomach contents are found largely occupied with pelagic squids, as large as the body of this shark in most specimens, small fishes including *Vinciguerria* (Photichthyidae), and crustaceans [1, 7, 8]. In its

feeding mechanism, we do not still understand enough; Jones [1] referred to only a few characteristic structures, which will be of help to scoop the flesh of prey and to induce the strong oral vacuum.

The purpose of the present paper is to describe anatomical features of the feeding apparatus of *Isistius brasiliensis* in detail and to compare with those of closely related groups. Also, we discuss these functions on the morphological basis.

MATERIALS AND METHODS

Examination of skeletons and muscles of *Isistius brasiliensis* was based on one male and four females. Several dalatiine species and other squaloids were dissected for comparison. Collection information of these specimens is listed below. Study materials are deposited in HUMZ (Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University) and FSFL (Far Seas Fisheries Research Laboratory, Shimizu, Japan). Definition of the Dalatiinae follows Compagno [5].

Dalatiinae

Isistius brasiliensis: one male—HUMZ 119287, 425 mm TL; four females—HUMZ 69173, 364

mm TL, HUMZ 86585, 480 mm TL, HUMZ 87120, 438 mm TL, HUMZ 89900, 516 mm TL.

Squaliolus aliae: HUMZ 119285, male, 185 mm TL.

S. laticaudus: two females—HUMZ 74972, 250 mm TL, HUMZ 74974, 245 mm TL.

Euprotomicrus bispinatus: HUMZ 90413, male, 197 mm TL.

Dalatius licha: two males—HUMZ 74603, 390 mm TL, HUMZ 95229, 621 mm TL.

Other squaloids

Deania quadrispinosum: FSFL-EE422, female, 325 mm TL.

Etmopterus lucifer: HUMZ 90230, male, 337 mm TL.

Oxyotus bruniensis: HUMZ 91383, male, 545 mm TL.

Somniosus microcephalus: HUMZ 112816, female, 1,425 mm TL.

Squalus acanthias: HUMZ 87733, male, 495 mm TL.

Zameus squamulosus: HUMZ 75872, male, 526 mm TL.

Figure drawings were made in the camera lucida image with dissected specimens stained by alcian blue. Anatomical terminology mainly follows Daniel [9] and Edgeworth [10].

Abbreviations used in figures are as follows:

alc —anterior upper labial cartilage
 am —adductor mandibulae
 ams —adductor m. superficialis
 bb —basibranchial
 bh —basihyal
 btp —basitrabecular process
 cb —ceratobranchial
 ch —ceratohyal
 chd —constrictor hyoideus dorsalis
 chv —constrictor hyoideus ventralis
 co —coracoid
 coa —coraco-arcuales
 cob —coraco-branchialis
 cod —constrictor dorsalis
 coh —coraco-hyoideus
 es —eye stalk
 fbc —articular fossa of basihyal with ceratohyal

fopp —foramen for ophthalmicus profundus
 gco —genio-coracoideus
 gcob — β -slip of genio-coracoideus
 gm —gum of upper jaw
 gop —groove for orbital process
 hb —hypobranchial
 hm —hyomandibula
 hmf —hyomandibular fossa
 hyp —hypaxial body muscle
 im —intermandibularis
 iow —interorbital wall
 jhm —joint cartilage of hyomandibula
 lf —lip fold
 lhc —ligamentum hyomandibulo-hyoideum
 llb —levator labialis
 llc —lower labial cartilage
 lmc —ligamentum mandibulo-hyoideum
 lpc —lip cover
 ma —mandibula
 mfl —mandibular flap
 mk —mandibular knob of mandibula
 op —orbital process
 opd —oral pocket
 pap —palatine plate of palatoquadrate
 pcm —pericardial membrane
 plc —posterior upper labial cartilage
 potp —postotic process
 pmg —posterior mouth groove
 pnf —posterior nasal fenestra
 pq —palatoquadrate
 proc —preoral cleft
 prop —preoral pouch
 qup —quadrate plate of palatoquadrate
 slc —fleshy sack of posterior upper labial cartilage
 so —suborbitalis
 sos —subotic shelf
 II —(foramen for) optic nerve

DESCRIPTION

In this section, external and internal characters of *Isistius brasiliensis*, which appear to accommodate its feeding mechanism directly or indirectly, are described and compared with the other members of Dalatiinae. The condition of the latter (or the other squaloid sharks if necessary) is noted in braces.

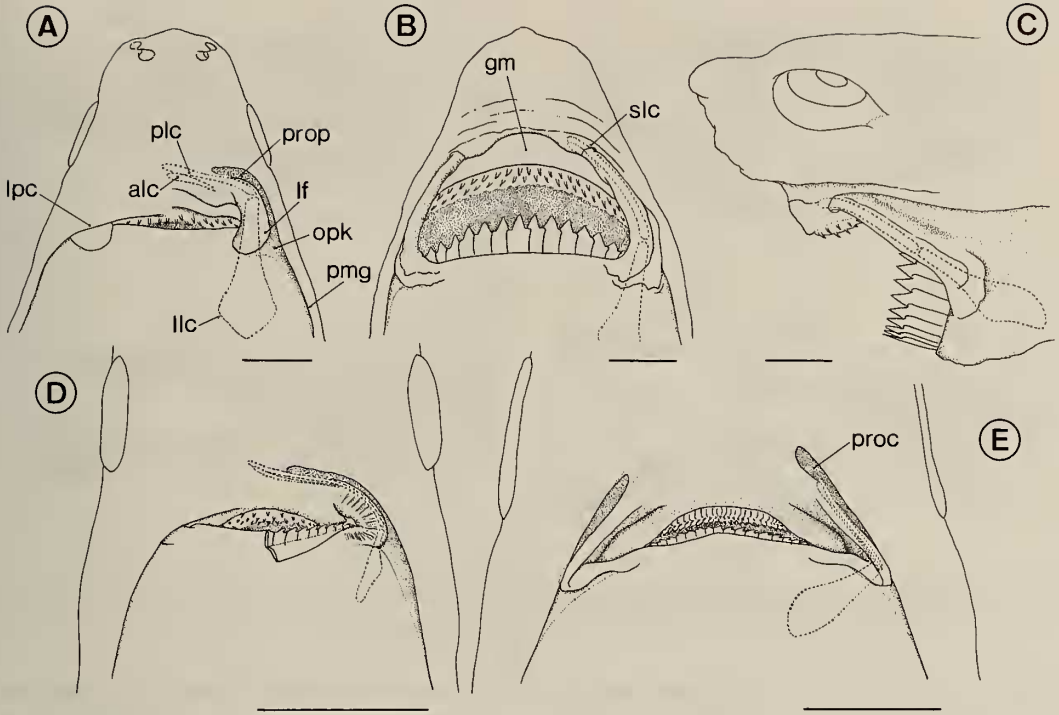


FIG. 1. Mouth structure of squaloids. A) ventral view of *Isistius brasiliensis* (the lip cover is deleted in right half); B) ventral view of same when jaws and lips are protruded showing the exposed gum of upper jaw and the lip sack for labial cartilages; C) lateral view of same; D) ventral view of *Squaliolus aliae* (the lip cover is deleted in right half); E) ventral view of *Deania quadrispinosum*. Scales are 10 mm.

Externals (Fig. 1)

The mouth of *Isistius* (Fig. 1A-C) resembles that of other dalatiines (Fig. 1D) in having a large cutaneous lip cover (lpc) and a thick and naked lip fold (lf) at the mouth corner. The lip cover is a skin continuing from the upper lip near the jaw symphysis to the posterior mouth groove (pmg), concealing a deep oral pocket (opk) and preoral pouch (prop); non-dalatiine squaloids have no lip cover, and the preoral pouch is exposed as the preoral cleft (proc; Fig. 1E). The lip fold is supported by a joint of the posterior upper and lower labial cartilages (plc, llc); in non-dalatiine squaloids (Fig. 1E), the lip fold also conceals another piece of labial cartilage (alc). The posterior mouth groove of *Isistius* is deep and extends posteriorly rearward to the half of distance from the corner of mouth to the first gill opening as in *Squaliolus* and *Euprotomicrus*.

In *Isistius*, the lip fold is stout with the smooth surface and conceals well-developed labial cartilages {lip fold is more or less lamellated, and labial cartilages are somewhat weak in other dalatiines (Fig. 1D)}. A gum in the upper jaw (gm) is considerably thickened, and a fleshy sack for the upper labial cartilages (slc) is made by the upper lip {such a bulky gum and the fleshy sack are absent}.

Skeleton

In the neurocranium of *Isistius* (Fig. 2A-B), the nasal capsule is somewhat reduced, but the orbit and otic capsule are well-expanded, with many modifications, e.g., an unusual opening of nasal capsule (pnf) at the subnasal fenestra, unchondrified interorbital wall around the foramen opticum (II), no eye stalk (es), and no subotic shelf (sos). Two conditions related to the jaw suspension are that: (1) the basitrabecular process (btp) is

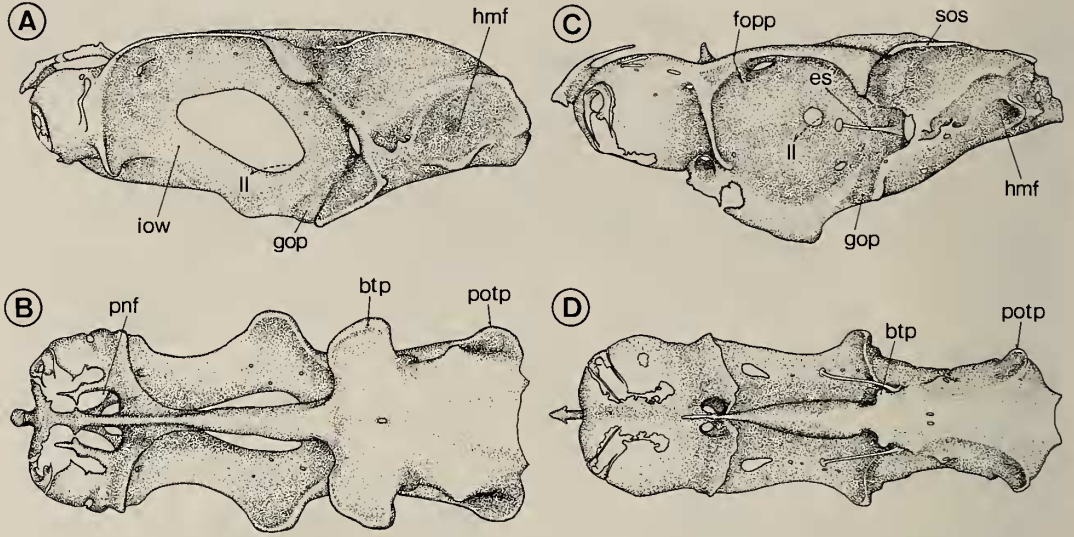


FIG. 2. Neurocrania of two dalatiines. A-B) lateral (A) and ventral views (B) of *Isistius brasiliensis*; C-D) lateral (C) and ventral views (D) of *Squaliolus laticaudus*. Scales are 10 mm.

expanded laterally to form a shelf below the posterior part of orbit {the basitrabecular process is only a small bulge supporting the orbital process of palatoquadrate (Fig. 2C-D)}; and (2) the postotic process (potp) is developed to form the dorsoposterior ridge of a deep hyomandibular fossa (hmf) {the hyomandibular fossa and postotic process are not so developed}.

The mandibular arch of *Isistius* (Fig. 3A-B, 4A-B) is characterized by fairly reduced upper and voluminous lower jaws, and it is noticeably different from that of other squaloids in the following respects: (1) the upper teeth are wholly inside the lower teeth when mouth is closed, and then they are not engaged each other {upper and lower teeth are engaged each other at least in part (Fig. 3D)}; (2) the palatoquadrate (pq) is composed of two thin and soft pieces, the anterior one (palatine plate: pap) is capable to warp dorsally, and the posterior one (quadrate plate: qup) have a minute orbital process (op) at its anterior end for the loose palatoquadrate-neurocranium articulation {the palatoquadrate is a single and stout cartilage with a higher orbital process, and the palatoquadrate-neurocranium articulation is firmer}; (3) the mandibula (ma; Meckelian cartilage) is thick and scoop-like, not curved laterally at the posterior

end {the posterior end of mandibula is somewhat curved laterally to form a fossa for the adductor mandibulae (am)}; (4) the mandibula has a flexible, weakly chondrified plate (mandibular flap: mfl) at its posteroventral edge {absent}; and (5) the ligamentum mandibulo-hyoideum (lmc) is very tough, inserted onto the posterior margin of mandibula near the joint between the hyomandibula and ceratohyal {this ligament is weaker and inserted onto the medial surface of the mandibula below the mandibular knob (mk) somewhat separated from the hyomandibula-ceratohyal joint}.

The jaw dentition of *Isistius* essentially resembles that of the dalatiines in having the dignathic heterodonty (Fig. 3); upper teeth are lanceolate arranging quincuncially and the lower teeth are with a large plate-like crown forming an interlocking tooth blade. In *Isistius*, the lower tooth rows almost extend to the point of jaw joint (articulation of upper and lower jaws) to form a semicircular saw as a fringe of the scoop-like lower jaw {the most posterior lower tooth is moderately separate from the jaw joint}. The lower teeth are enormously large and have a triangular, fully erected cusp without a regular serration {lower teeth have a more or less inclined cusp with or without serration}. In contrast, upper teeth are weak, and

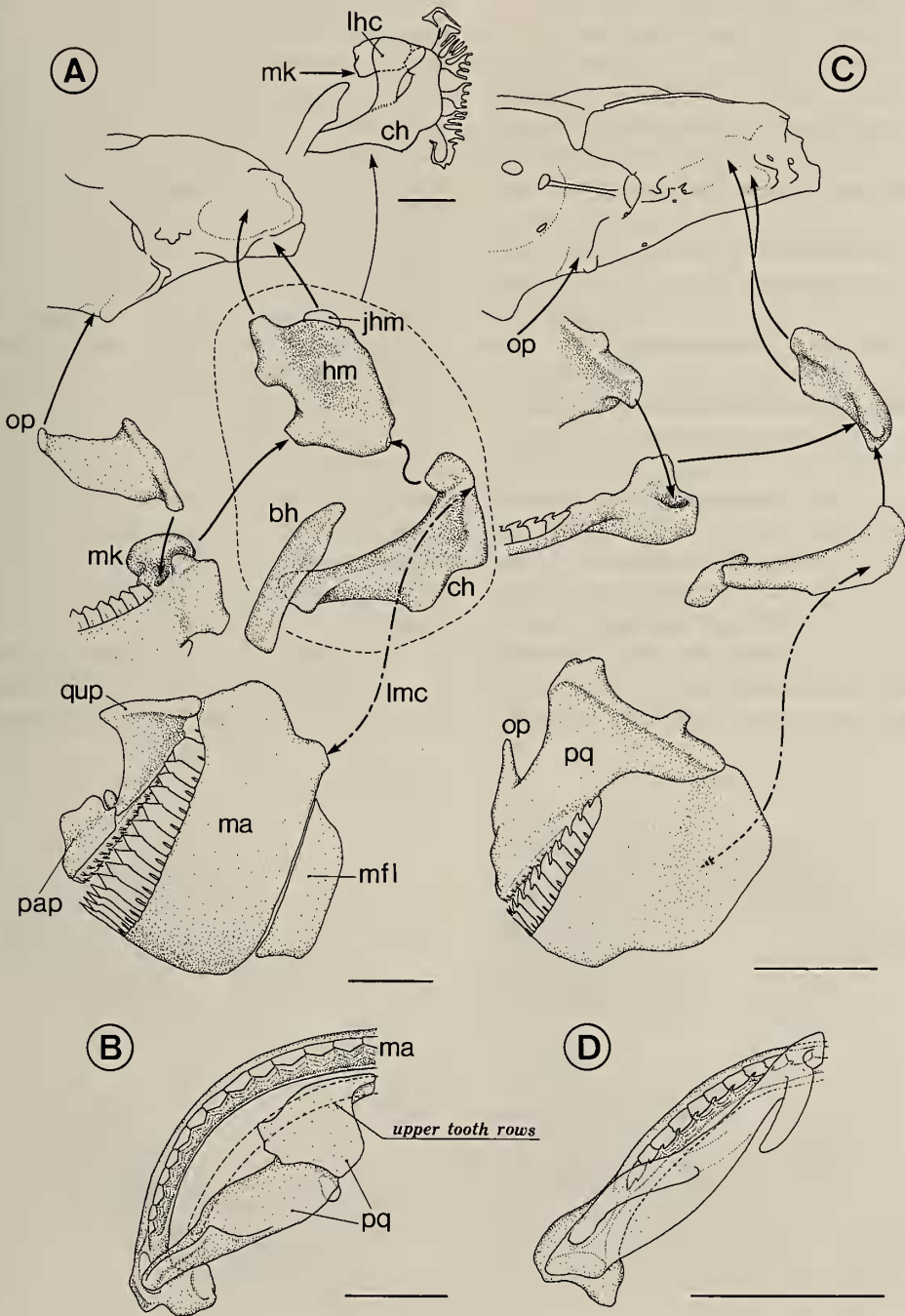


FIG. 3. A) Neurocranium and mandibular and hyoid arches of *Isistius brasiliensis* showing jaw suspension (the hyomandibula is drawn from dorsal view), and lateral view of hyoid arch as inset (right upper); B) dorsal view of mandibular arch of *Isistius brasiliensis*; C) same as (A) in *Squaliolus laticaudus*; D) same as (B) in *Squaliolus laticaudus*. Scales are 10 mm.

the functional tooth rows are not supported by the palatoquadrate in part {upper tooth rows are entirely supported by the palatoquadrate}.

The hyoid arch (Figs. 3A, 5A) of *Isistius* is also modified considerably. The hyomandibula (hm), like *Dalatias*, is short, flat, and directed laterally, not inclined posteriorly {the hyomandibula is somewhat longer, compressed, and directed postero-latero-ventrally (Fig. 3C)}. The proximal terminus of hyomandibula is bifurcate, and its posteroventral condyle is composed of a separate cartilaginous piece (jhm) {it is also slightly bifurcate, but without a separate cartilage}. The distal terminus of hyomandibula has a small expansion to receive the mandibular knob of mandibula (mk) at its anterior edge and a simple depression for the articulation with the ceratohyal at its posterior edge. Thus, the hyomandibula-ceratohyal articulation is somewhat behind the mandibula-hyomandibula articulation {this feature is also seen in *Dalatias*, but not so separate as in *Isistius*; the distal terminus of the hyomandibula is distinctly bifurcate for the articulation with the ceratohyal, and the hyomandibula-ceratohyal articulation is very close to the mandibular knob}. The ceratohy-

al (ch) of *Isistius* is very stout, connected with the hyomandibula by a thick ligament (ligamentum hyomandibulo-hyoideum: lhc); this ligament arises from the basicranium below the hyomandibular fossa, covering the posterodorsal surface of the hyomandibula, and it is inserted on the anterodorsal surface of ceratohyal {the ceratohyal is also developed, but such a ligament is absent except *Dalatias*}. The large quadrangular basihyal (bh) has a simple concavity (fbc) at its posteroventral surface to receive the anterior terminus of the ceratohyal (Fig. 5A) {the basihyal is smaller, generally trapezoid in shape, and the fossa for articulation with the ceratohyal is situated on its posterolateral margin (Fig. 5B-C)}.

Isistius has strongly reduced branchial arches, and the basibranchial copula (hypobranchials plus basibranchials) is almost absent (Fig. 5A). The first ceratobranchial (cb1) is not articulated with the basihyal, situated far posterior from it {in *Dalatias*, the ceratobranchial-basihyal articulation is also absent, but the first ceratobranchial is supported by the hypobranchial as a transverse bar (hb1: Fig. 5C); in other squaloids, the first ceratobranchial is connected with the basihyal tightly or loosely (Fig.

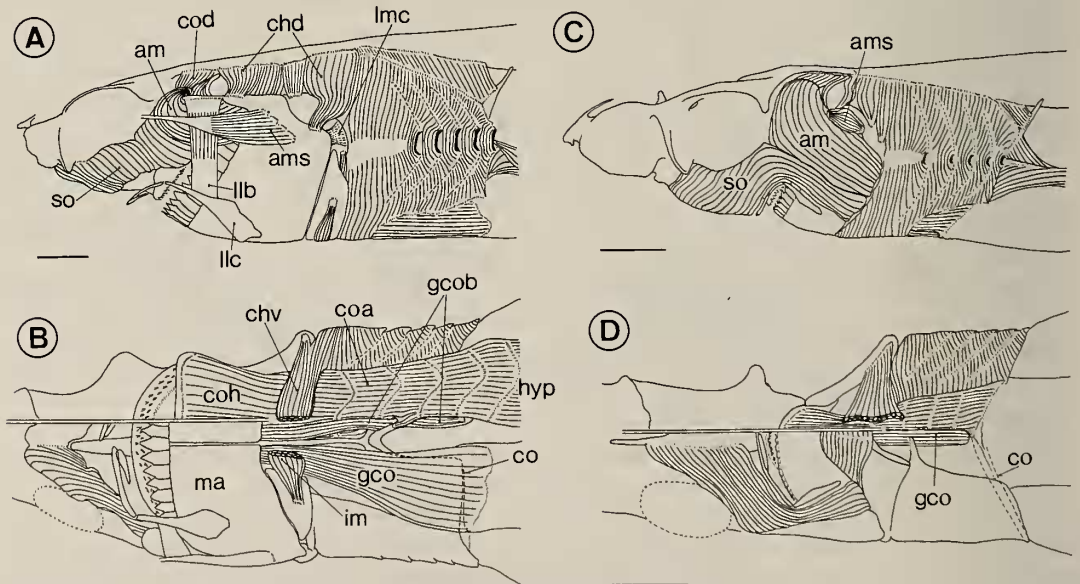


FIG. 4. Head musculature of two dalatiines. A-B lateral (A) and ventral views (B) of *Isistius brasiliensis*; C-D) lateral (C) and ventral views (D) of *Squaliohus laticaudus* (B and D: mandibula is removed in upper half, above double solid line). Scales are 10 mm.

5B)}. *Isistius* is unique in having an elongate separate hypobranchial in the fifth arch (hb5), to which the large, paddle-shaped ceratobranchial (cb5) is loosely connected {the fifth arch does not have a discrete hypobranchial}. The gill raker is completely absent {present in most other squaloids}.

The shoulder girdle (Fig. 4B) of *Isistius* is characterized by the fragile and curiously curved coracoid (co). It courses medially for a short distance, turns anteriorly at a right angle, and extends anteroventrally to form a peculiar hairpin turn at the symphysis that forms the pericardial floor {the coracoid bar is a stout transverse bar, and this is not strongly curved (Fig. 4D)}.

Musculature

The mandibular muscles (Fig. 4A-B) are also modified in *Isistius* as follows: (1) the adductor mandibulae (am) is very reduced, and its insertion onto mandibula is restricted slightly below the jaw joint via tough tendinous tissue {the adductor mandibulae is housed at the whole posterior half of mandible (Fig. 4C)}; (2) the thick suborbitalis (so) is inserted onto the tendinous tissue of the adductor mandibulae {the suborbitalis is inserted onto the anterior part of mandibula with (*Dalatias*) or

without (*Euprotomicrus* and *Squaliolus*) a tendon for insertion (Fig. 4C-D)}; (3) the adductor m. superficialis (ams) is completely separate from the adductor mandibulae, arising from the outer surface of the mandibula {this muscle is usually a subdivision of the adductor mandibulae, situated on the otic process of palatoquadrate}; (4) a unique thin muscle, the levator labialis (llb), arises from the otic process of palatoquadrate and is inserted on the medial edge of the posterior mouth groove {absent}; and (5) the anterior and posterior extremities of the constrictor hyoideus dorsalis (chd) are inserted on the mandibula {the anterior edge of this muscle is inserted onto the palatoquadrate, not reaching the mandibula}.

The hypobranchial longitudinal muscles, occupying the space below the oral cavity and pharynx, are noticeably modified in *Isistius*. The genio-coracoideus (gco) is thin and broad, tapering forward, and originates from the ventral surface of the hypaxial muscle below the origin of pectoral fin (Fig. 4B). Another slip of muscle (gob), arising from the anterior curved surface of the coracoid and inserted onto the mandibula with the genio-coracoideus, is present (genio-coracoideus β) {the genio-coracoideus is an unpaired, narrow muscle bundle that arises from coracoid symphysis or

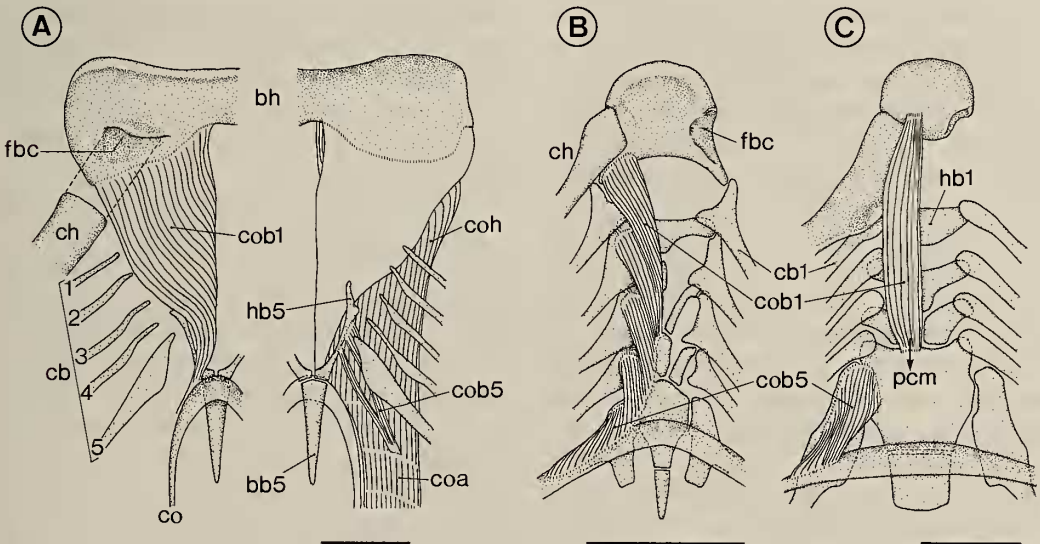


FIG. 5. Basal portion of hyoid and branchial arches with the coraco-branchiales of three dalatiines. A) *Isistius brasiliensis* (left—ventral view showing the coraco-branchialis 1; right—ventral view showing the coraco-branchialis 5; B) *Squaliolus laticaudus* (ventral view); C) *Dalatias licha* (ventral view). Scales are 10 mm.

pericardial membrane, and the genio-coracoideus β is absent (Fig. 4D)}. The rectus cervicis, often subdivided into the anterior (=coraco-hyoideus: coh) and posterior halves (=coraco-arcuales: coa), is expanded well and is directly connected with the hypaxial muscle posteriorly {the rectus cervicis arises from the coracoid, and is not directly connected with the hypaxial muscle}. The coraco-branchiales (cob) are simplified, composed of two slips (Fig. 5A); one (cob1) is a wide and flat, arising from the pericardial membrane and inserted on the basihyal; the other (cob5) originates on the dorsal side of the fascia of coraco-arcuales, and its insertion is on the fifth hypobranchial and ceratobranchial {the coraco-branchiales are composed of five slips (Fig. 5B); their origins are the fascia of rectus cervicis (first) and the pericardial membrane or the anterior surface of coracoid (others), and insertions are, from front, the basihyal, the ceratobranchial and hypobranchial of the second, third, fourth, and fifth arches; *Dalatias* (Fig. 5C) also has two separate coraco-branchiales like *Isistius*, but the posterior slip arises from the coracoid}.

DISCUSSION

We can often find crater wounds on the surface of tunas and swordfishes in a fish market (Fig. 6). It is round or oval with the size of 5 cm by 7 cm at the most. Jones [1] discussed the probability of the relation between this wound and the feeding mechanism of *Isistius*. His arguments on the feeding function of this shark are summarized as follows:

- (1) *Isistius* gives such a wound by pushing its lower tooth row against the body of prey and then scooping the flesh. In his experiment with a dead fish, the scoop-like lower teeth of *Isistius* can produce a crescentic wound, which is very similar in size and shape to that often observed in tunas caused by the incomplete attack.
- (2) *Isistius* can make a strong oral vacuum when the tongue (basihyal) is pulled back by the voluminous throat muscle (rectus cervicis). Concurrently, the shark closes its spiracles and protrudes lips completely around the mouth.
- (3) The body rotation should be facilitated by the

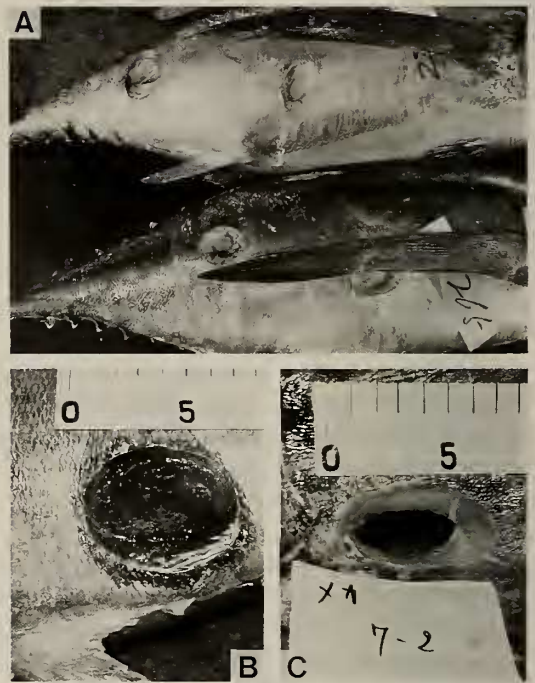


FIG. 6. Crater wounds on sides of tunas and swordfish at the Kesennuma Fish Market, Miyagi prefecture, Japan (A-B, *Tunnus alalunga*; C, *Xiphias gladius*). A wound in (C) penetrates into the body cavity. Each wound is 5 to 7 cm in a major axis. (B and C: photo by Toshiro Chiba).

drag of water when *Isistius* heads on the prey as expected in many examples. At the next moment, the body of *Isistius* would rotate around the point of attachment until the shark is oriented in the same direction as the prey. The crater wound is then completed.

Morphological features of this shark can explain these functions, as mentioned below.

On the first hypothesis, Jones [1] noticed the peculiarity of dentition in *Isistius*. This shark shares a typical dignathic heterodonty with many other squaloids, which should work for the clutching-cutting-type feeding habit [11]. Squaloid sharks (Figs. 3C, 4C) generally hold food items by the teeth of both jaws, and cut them by sharp lower teeth. Developed adductor mandibulae plays the main role in this function. In *Isistius* (Figs. 3A-B, 4A-B), upper and lower teeth cannot be engaged each other. Upper and lower jaws are ill-balanced in size, and the palatoquadrate is

subdivided into the anterior and posterior halves. The adductor mandibulae is small, not widely inserted on the lateral surface of lower jaw. At the collision with a prey, the lower jaw is given a strong shock (reaction of the collision), but it must keep the appropriate angle to penetrate the flesh with the lower teeth. The massive suborbital muscle, with the reduced adductor mandibulae, appears to support this function.

In contrast with the tough lower teeth, the role of upper teeth seems rather moderate. Jones [1] observed several scratches produced by *Isistius*'s upper teeth. These are opposite to a crescentic wound caused by lower teeth, at barely inside the crater if this attack were complete. The flexible upper jaw might be bent at the middle portion to make the oral area greater at the collision. Upper teeth are thus effectively anchored on the prey to prevent the shark body whisked off during the gouging.

Such unique jaw morphology is apparently not suited to clutch and masticate foods. The scoop-like tooth row of the lower jaw along the ventral surface of body thus appears more appropriately designed to gouge out the flesh of prey as sug-

gested by Jones [1]. *Isistius* usually feeds small pelagic fish and squids [1, 7, 8], and this scooping function also should occur for these small preys.

Second, Jones [1] explained that the strong oral vacuum is induced by the function of a large basihyal, the developed rectus cervicis, spiracles, and lips. Thickened labial fold and gum in the upper jaw and the flexible upper jaw must be useful to fit the oral margin to the shape of food. We found the unusually curved shoulder girdle, and this allows the rectus cervicis directly contacts with the thick hypaxial muscle. The oral vacuum will be thus induced by the contraction of whole ventral muscle of body. We also noticed that the basal portion of branchial arches is incomparably reduced, especially in the separation between the first ceratobranchial and basihyal. This must be concerned with stronger and smoother retraction of the basihyal.

Isistius has another mechanism to make the stronger oral vacuum with ingenuity (Fig. 7). In most shark groups, the lower jaw is lowered mainly by the function of the whole hyoid arch and muscles inserted onto the basihyal (rectus cervicis and coraco-branchialis 1). As shown in Figure 7C,

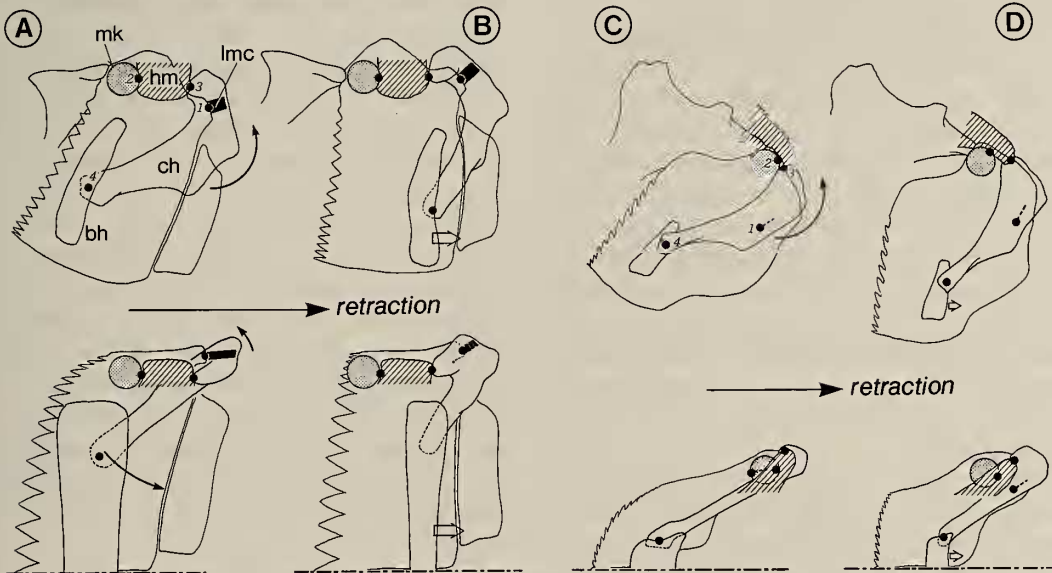


FIG. 7. Diagrams of the retraction of basihyal and movements of the associated parts of (A-B) *Isistius* and (C-D) *Squaliolus* (upper—lateral view; lower—dorsal view). Black dots show the following points: 1, the ligamentous connection between ceratohyal and mandibula; 2, the articulation between mandibular knob and hyomandibula; 3, the hyomandibula-ceratohyal articulation; and 4, the basihyal-ceratohyal articulation.

the ligamentum mandibulo-hyoideum is usually short and fastens the ceratohyal and mandibular rigidly (point 1) somewhat below the hyomandibula-ceratohyal articulation (point 3). The point 3 is the center of rotation of the ceratohyal, and it is very near the center of rotation of the mandibula (point 2). When the basihyal is retracted (Fig. 7D), therefore, the mandibula will be lowered at the almost same degree as the rotation of ceratohyal, and the oral cavity does not expand so strongly. In *Isistius* (Fig. 7A), the point 3 is characteristically posterior to the point 2 by the width of hyomandibula. The ligamentum mandibulo-hyoideum (1) joins the posterior margin of mandibula with the ceratohyal near the hyomandibula-ceratohyal articulation (3). The anterior part of ceratohyal thus can be somewhat free from the mandibula. Moreover, the basihyal has a semi-globate fossa for the articulation with ceratohyal (point 4), and it gives the flexibility to the basihyal-ceratohyal articulation. When the basihyal is pulled back (Fig. 7B), the anterior end of the ceratohyal can swing posterointernally like man's wrist when elbows are spread out. Therefore, the basihyal can move backward more strongly than the lowering of mandibula, and the oral cavity is expected to be more enlarged than the other squaloids.

The bigger the oral cavity is, the stronger the oral vacuum should be induced. The shape and size of mandibula and basihyal clearly show that *Isistius* essentially has a larger oral cavity. The movement of ceratohyal mentioned above will serve to expand it further. In addition, the modification of the hyomandibula should be also related with this function. This cartilage is directed posterolaterally when the mouth is closed and has a separate cartilaginous piece at the proximal end. The hyomandibular fossa on the otic capsule is well developed. These structures probably make the hyomandibula lower more strongly to enlarge the oral cavity.

On the third hypothesis (mechanism of body rotation), Jones [1] explained that *Isistius* utilizes the locomotion of prey and the drag of water for gouging. It is reasonable for the fast swimmers. However, *Isistius* attacks the slower fishes and cetaceans, and even the dead fishes. Almost all the wounds on tunas and swordfishes we observed

were so fresh with bleeding that these wounds would have been given after they were restrained by the fishing gear (long line) or dead on hooks (Fig. 6). The body rotation of *Isistius* should be thus more spontaneous than Jones considered. The body itself must be twisted by the differential contraction of right and left body muscles.

We consider that these three basic functions for feeding occurs in a very moment. This small shark stabs the prey with the sharp lower teeth at the collision. Immediately after this, the ventral body muscle must be suddenly contracted to pull the basihyal back and the oral vacuum is induced in order to stick the mouth to the prey. The contraction of body muscle should simultaneously create a twisting moment of the body itself with or without the help of the drag of water. A half turn of body probably makes a complete crater-like wound.

Two dwarf dalatiine shark genera, *Euprotomicrus* and *Squaliolus*, have the similar habitat and outlook to *Isistius*, and these were often compared with each other [8, 12, 13]. The feeding mechanisms of *Euprotomicrus* and *Squaliolus*, however, should be the typical squaloid-type (clutching-cutting type) [11], because their feeding apparatus is essentially same as that of squaloids. *Isistius* rather share some characteristic conditions in the feeding apparatus with another dalatiine shark, *Dalatias licha*, i.e., the hyomandibula-ceratohyal articulation somewhat behind the mandibular knob, the first ceratobranchial widely apart from the basihyal, and reduced coraco-branchiales composed of two muscle slips. However, *Dalatias*'s palato-quadrates, arrangement of upper and lower tooth rows, basihyal, and related musculature are well similar to those of other squaloids, and it is unlikely that it takes same feeding manner as *Isistius* does. Two other rare dalatiine sharks, *Euprotomicroides* and *Heteroscymnoides*, whose feeding apparatus is hardly known, cannot scoop out the flesh of fish either because of their typical dalatiine dentition [5, 14]. A culprit of the crater wound is thus clearly identified, the cookie-cutter shark.

ACKNOWLEDGMENTS

We would like to thank Kunio Amaoka (Laboratory of

Marine Zoology, Faculty of Fisheries, Hokkaido University) who gave us considerable support and suggestions during this study. We are also indebted to Stuart G. Poss (Gulf Coast Research Laboratory Museum, Ocean Springs) for constructive reading of the manuscript. Toshiro Chiba (Kesenuma City) kindly took photographs of crater wounds. Keiichi Matsuura, Richard Rosenblatt, "H. J." Walker, Jr., Yasunori Sakurai, Shigeyuki Kawahara, and Harumi Yamada provided specimens for comparative studies.

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